

The University of Chicago

ANATOMY OF THE SEEDLINGS OF
ASPARAGUS OFFICINALIS

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR
OF PHILOSOPHY

DEPARTMENT OF BOTANY

1934

By
NAOMI MULLENDORE

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ANATOMY OF THE SEEDLING OF ASPARAGUS OFFICINALIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 466

NAOMI MULLENDORE

(WITH FORTY-FOUR FIGURES)

Introduction

Of the works published concerning *Asparagus officinalis* L., some, such as those of ROBBINS (11) and JONES and ROSA (9), have dealt chiefly with the cultural and commercial aspects rather than with the morphological ones. BORTHWICK (4), ROBBINS and BORTHWICK (12), COOLEY (5), and BLASBERG (3) have used morphology largely as a basis for physiological study. Some of these have dealt with limited phases, BORTHWICK (4) and ROBBINS and BORTHWICK (12) with germination; COOLEY (5) with reserve cellulose of the seed. BLASBERG (3) has given some attention to anatomy. His work included growth habit, seedling development, root structure, and stem structure. SCHOLZ (13) has discussed morphology but has not given the detail of the development of the lateral roots and the root-stem transition. ARBER (1) has discussed the cladophylls and leaves. POESE (10) has dealt with the concentric and collateral vascular bundles of the rhizome and stem. BERNÁTSKY (2) has explained the development of the rhizome and the succeeding spears, and something of general structure. ZWEIGELT (17) has compared the members of the Asparagoideae on an anatomical basis.

The present study concerns itself with the details of the anatomy of the seedling, only parts of which have been reported previously:

Material and methods

In April, 1932, seeds of asparagus of the Mary Washington variety were obtained from Coker's Pedigreed Seed Company of Hartsville, South Carolina. To hasten germination, the seeds, after sterilization in 0.25 per cent Uspulun solution, were soaked in distilled water for three days in an incubator at approximately 30° C., the optimum

pre-germination time and temperature for soaking recommended by BORTHWICK (4). Although many seeds are injured by long soaking, especially at low and high temperatures, COUPIN (6) found asparagus seeds strongly resistant to immersion in water. Most of these seeds were planted out-of-doors in a loamy garden soil. To observe germination more closely, some were placed on moistened filter paper in sterilized petri dishes.

After germination began, seedlings were removed at intervals, killed and fixed chiefly in formalin-alcohol and in formalin-acetic-alcohol. Better fixations were obtained in the latter.

Following a suggestion of Dr. H. E. HAYWARD, it was found that heat would loosen the embryos from the soaked seeds so that they could be readily extracted. This made it possible to obtain the embryo from the hard endosperm more easily and with less injury than by dissection. Most of the embryos were obtained by heating in water to a temperature slightly below the boiling point, although no apparent injury resulted from heating the seeds to the boiling point.

The usual procedure for the paraffin method was followed, except that, to soften the lignified tissues, older parts of the plant were treated with 48 per cent hydrofluoric acid from one to five days before dehydration. A modification of the n-butyl alcohol method (16) was used in dehydrating these tissues.

Sections were cut 10 μ thick and stained in a modification of Flemming's triple stain. Detailed drawings were made by aid of a camera lucida and a microprojector.

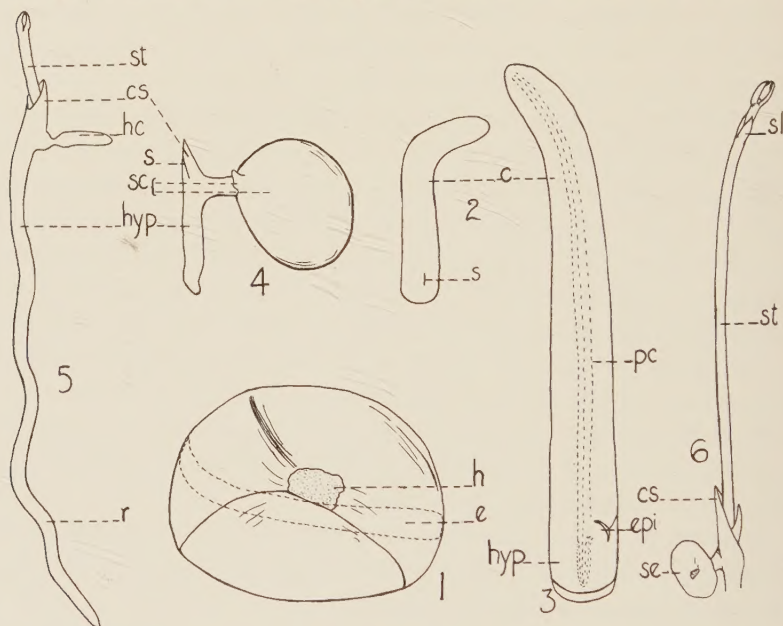
Investigation

SEED AND EMBRYO

The ripe seed, covered with a black coat, the surface of which is finely rugose, is somewhat spherical or subglobose, rounded on the side away from the hilum, but flattened somewhat along one side of the hilum, producing a triangularly pyramidal effect on that side of the seed (fig. 1).

Most of the mature seed is composed of a hard cartilaginous endosperm with walls of hemicellulose (12, 5). The slender embryo, 3-4 mm. long, consisting chiefly of the haustorial cotyledon, is imbedded in the endosperm (fig. 1). There is generally a slight curve in the

distal portion of the cotyledon, although some very short embryos are nearly straight. The embryo is blunter at the basal end, tapering gradually to the distal end of the cotyledon. There is a longitudinal slit in the cotyledon about 0.25 mm. in length, located just above the cotyledonary plate (fig. 2). Through this slit, the margins of which represent the edges of the cotyledonary sheath, the shoot will emerge. The tissues of the cotyledon distal to the slit consist of an



FIGS. 1-6.—Fig. 1, seed showing position of embryo. Fig. 2, embryo dissected from seed. Fig. 3, diagram of longitudinal section of embryo. Fig. 4, young seedling showing conelike development of cotyledon. Fig. 5, seedling with haustorial portion of cotyledon dissected from seed. Fig. 6, part of older seedling (*h*, hilum; *e*, embryo; *s*, slit; *sc*, seed coat; *hyp*, hypocotyl; *epi*, epicotyl; *c*, cotyledon; *pc*, procambial strand; *r*, root; *cs*, cotyledonary sheath; *hc*, haustorial part of cotyledon; *sl*, scale leaf; *st*, stem; *se*, seed).

outer layer of papillate, densely protoplasmic, glandular cells; a region of six to ten rows of parenchymatous cells; usually three, sometimes four, procambial strands; and a central parenchyma. The epicotyl is a hemispherical mass of embryonic tissue at the base of the cotyledon within the small chamber below the slit (fig. 3). The short hypocotyl has five or six xylem and as many phloem strands alter-

nately arranged, surrounding a pith. The xylem is generally not lignified. A single layer of pericyclic cells surrounded by the endodermis, ten to fifteen layers of cortical cells, and a single layer of epidermal cells complete the structure of the hypocotyl.

GERMINATION AND YOUNG SEEDLING

The tip of the hypocotyl lies very near the margin of the seed coat. Upon germination it emerges, tearing out a rounded disc of the seed coat, which, however, remains attached at one point. The basal portion of the cotyledon bearing the slit also emerges and enlarges so that it appears as a conelike structure which incloses the epicotyl (fig. 4). As development proceeds, there appears on the axis inside the cotyledonary sheath the first scale leaf. The next internode elongates appreciably so that the apical meristem and the leaf primordia it bears are brought well above the cotyledonary sheath and the first leaf (figs. 5, 6). The second and third leaves may exhibit a one-half phyllotaxy; the upper leaves are arranged in the two-fifths phyllotaxy. Growth of the parenchymatous cells of the haustorial portion of the cotyledon, by absorption of the surrounding endosperm, proceeds until the cotyledon almost fills the seed coats.

HYPOCOTYL AND PRIMARY ROOT

In the hypocotyl there are five or six protoxylem strands alternating with as many phloem strands. Metaxylem is differentiated toward the center surrounding a small pith and can be found in seedlings in the earliest stages of germination (fig. 7). Extensions from the lower portion of the hypocotyl develop into the primary root and possess the same arrangement of tissues. As the root matures the metaxylem differentiates at the central region until no parenchyma is left. Thus is formed the exarch radial protostele (fig. 8). The protoxylem consists of small thick-walled cells with spiral thickenings. The phloem is composed of sieve tubes, many small companion cells, and phloem parenchyma. The pericycle is limited to a single layer of large thin-walled cells. The endodermis has, at first, only small thickenings on the radial walls. Later the thickenings may extend to the inner tangential walls. The cortex consists of eight to twelve layers of cells, the outermost layer of which becomes suberized.

Development of the root axis is produced by two histogenic layers. This agrees with TREUB's findings (14) and represents a variation from type 2 of JANCZEWSKI (8). In the root tip in the Liliaceae TREUB found only two groups of distinctly separate initials: (1) the initials of the plerome, which are usually very few in number; and (2) a group of many cells outside of these, which serve as common initials for periblem, dermatogen, and cap (fig. 9). These latter ini-

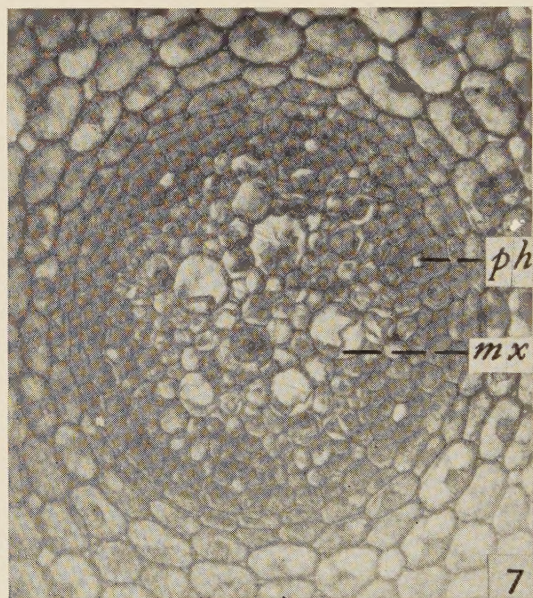
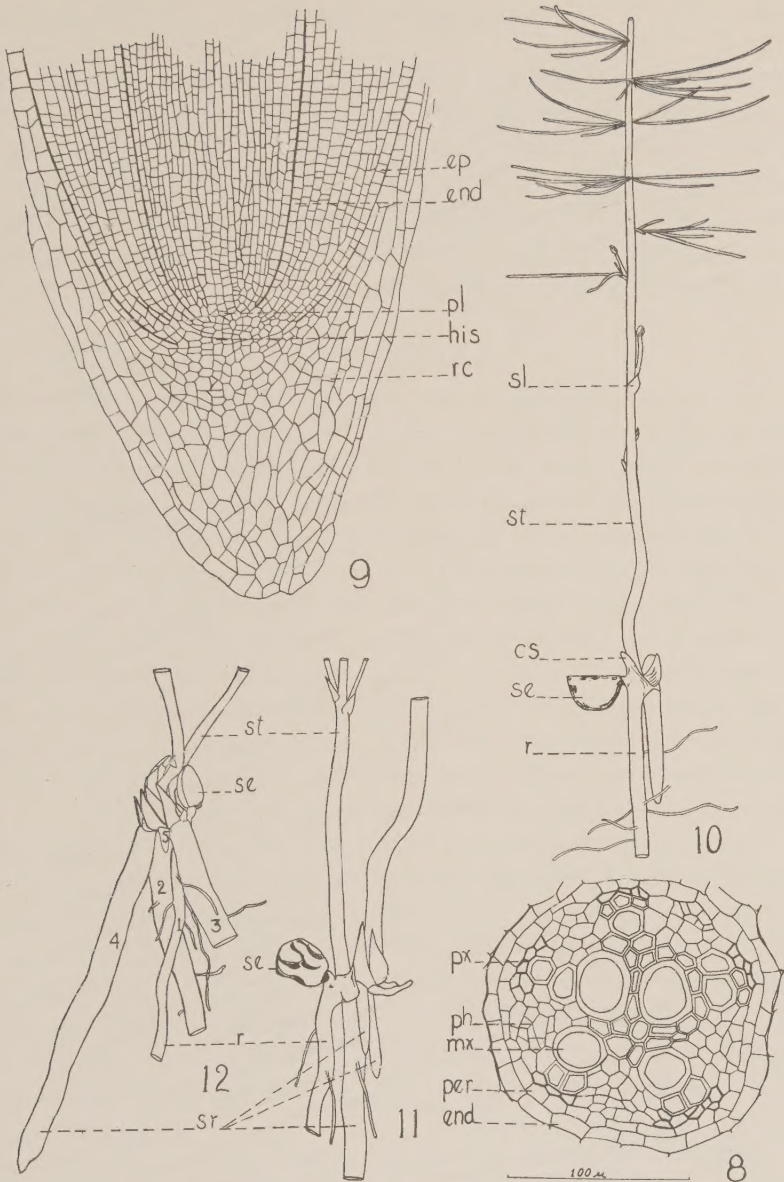


FIG. 7.—Transverse section of stelar region of primary root 1 mm. from root tip (*ph*, phloem; *mx*, metaxylem).

tials give the appearance of a general meristematic region from which new cells are derived with little regularity. Although rows of cells of the cortex and the epidermis may be traced into this region, the rows of cells of the cap are soon indistinguishable owing to irregular divisions of cells.

The mature primary root, less than 1 mm. in diameter and rarely more than 2 dm. in length, may persist throughout the first growing season, although its functions may largely be replaced by those of the large storage roots. The latter arise, apparently without any



FIGS. 8-12.—Fig. 8, transverse section of exarch, radial protosteles of primary root. Fig. 9, median longitudinal section of primary root. Figs. 10-12, portions of seedlings to show arrangements of parts (*ph*, phloem; *px*, protoxylem; *mx*, metaxylem; *per*, pericycle; *end*, endodermis; *ep*, epidermis; *rc*, root cap; *pl*, plerome; *his*, histogen for cortex, epidermis, and root cap; *se*, seed; *cs*, cotyledonary sheath; *st*, primary stem; *r*, primary root; *sl*, scale leaf; *sr*, storage roots).

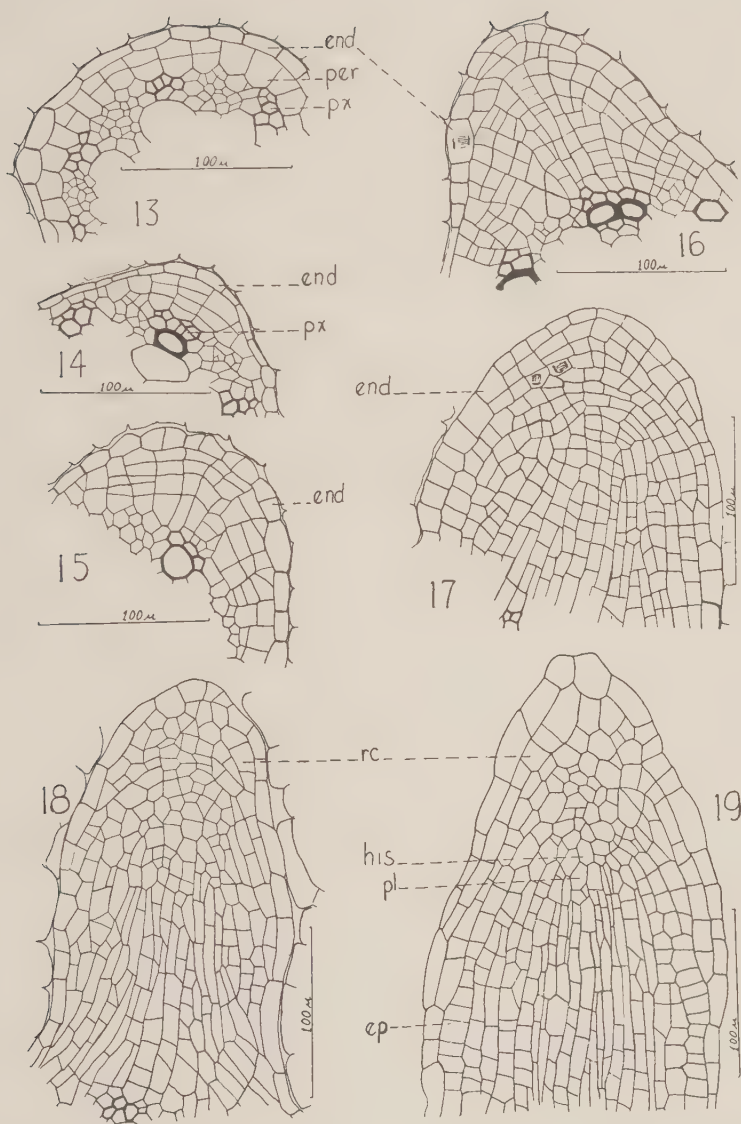
order, from the lower side of the developing rhizome with such frequency and compactness that they become very crowded as the massive crown develops (figs. 10-12). These fleshy roots, with a diameter two to six times greater than the primary root, possess a pith, a large number of alternating xylem and phloem strands, and an extensive development of cortical tissue. The outer rows of cells of the cortex become thick-walled and suberized.

LATERAL ROOTS

Lateral roots originate in the pericyclic region of the primary root before the thickening of the walls of the large metaxylem vessels occurs. These branch roots are first noted as meristematic activity of the pericyclic cells usually directly opposite the protoxylem point. The first division of the pericycle is a tangential one (fig. 13). This is followed by other tangential divisions until four to six rows of cells are formed, when radial divisions also occur (figs. 14, 15). These divisions occur somewhat irregularly, but the cells tend to be laid down in rows parallel to the radial walls of the original pericyclic cells. Continued divisions of the pericycle produce a conical mass of meristematic tissue (figs. 16, 17). A secondary root halfway through the cortex of the primary root shows differentiation into two histogenic regions as found in the primary root (figs. 18, 19).

At about the time the first tangential divisions of the pericycle occur, the endodermal cells defining the tip of the root elongate and increase in size, keeping pace with the development of the pericycle (fig. 14). When radial divisions of the pericyclic cells occur, the endodermis over the developing root tip also undergoes radial divisions (fig. 15). Radial divisions of the endodermis are followed by tangential ones (figs. 16, 17), and by this means a considerable portion of the "temporary" root cap is derived from the endodermis (figs. 18, 19).

Lateral roots extend through the cortex partly by mechanical pushing and partly by digestion of the older cortical cells. The first is evidenced by the crushed cortical cells about the young root tips. In later stages there is a lack of accumulated debris about the tip of the secondary root, which may be considered as evidence that diges-



FIGS. 13-19.—Transverse sections of portions of young primary roots showing origin of lateral roots (*px*, primary xylem; *per*, pericycle; *end*, endodermis; *ep*, epidermis; *pl*, plerome; *his*, histogen for cortex, epidermis, and root cap; *rc*, root cap).

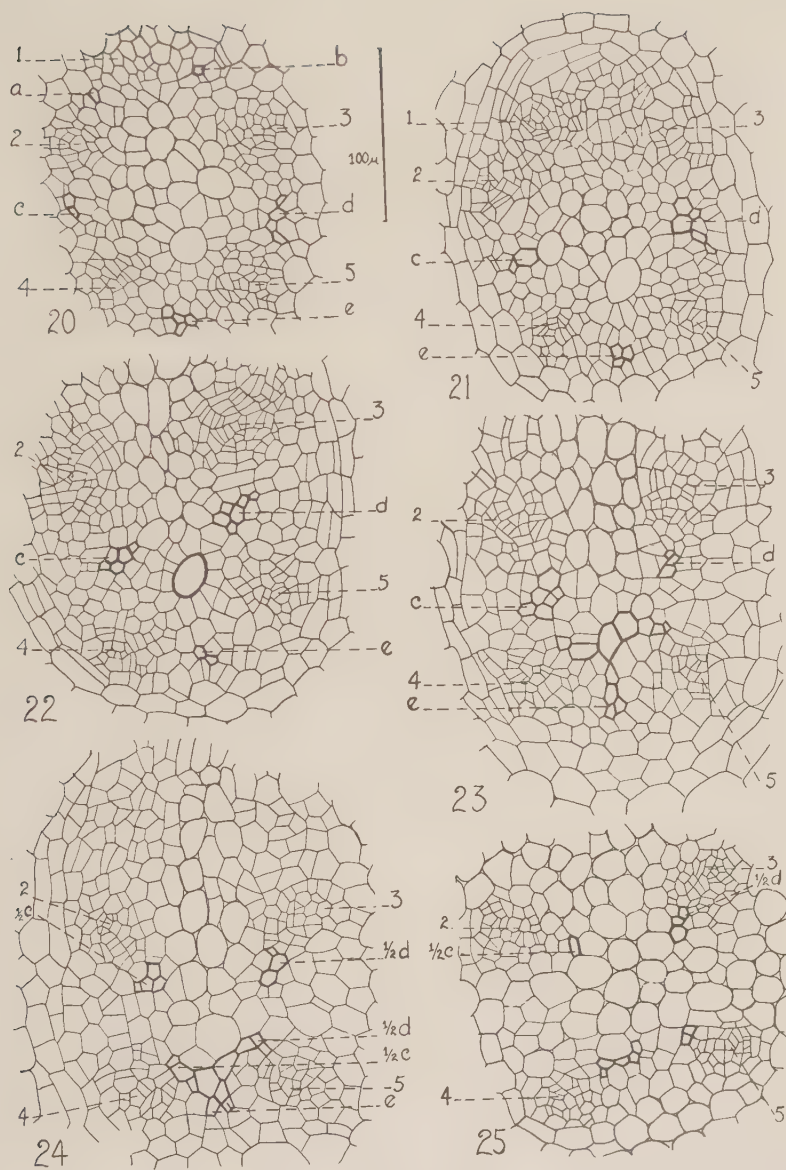
tion is important in the passage of secondary roots through the cortex.

These secondary roots continue development and extend beyond the limits of the primary roots as fibrous branches. They are usually triarch, with one large metaxylem vessel at the center.

TRANSITION REGION OF YOUNG EMBRYO

In a young embryo the cotyledon and the epicotyl are more or less in the same straight line, and in a longitudinal section the epicotyl appears as a somewhat lateral structure. Owing to the slight development of the epicotyl and the fact that very little conductive tissue is differentiated at this early stage within it, the transition must be determined largely as it takes place in the upper region of the hypocotyl and the cotyledon.

In a series of sections of a young embryo about 4 mm. long, in which the epicotyl is still only slightly developed, the transition from hypocotyl to cotyledon is evident. The orientation of the stelar tissues at successive levels from hypocotyl to cotyledon depicts the transition from the radial arrangement in the hypocotyl to the collateral arrangement in the cotyledon. A transverse section through the hypocotyl about $180\ \mu$ below the base of the epicotyl has the typical radial arrangement of the stelar structure. For convenience in following the orientation of tissues, the individual phloem and xylem strands have been given numbers and letters (fig. 20). All the xylem strands are not equally well differentiated, since the three (*c*, *d*, *e*) opposite the region which is directly below the apparently slightly lateral epicotyl are larger. A transverse section $80\ \mu$ higher includes the base of the cotyledonary sheath and the tissue just below the base of the epicotyl (fig. 21). The two weaker xylem strands (*a*, *b*) are not differentiated at this level, and xylem strands *c*, *d*, and *e* are slightly nearer the center. The phloem maintains its relative positions. At a still higher level, $100\ \mu$ above the first previous section, phloem strand 1 extends toward the base of the epicotyl. Extensions from the phloem strands 2 and 3, located right and left of 1, also are differentiated in the direction of the base of the epicotyl. The three stronger xylem strands (*c*, *d*, *e*) are nearer the center than in the previous section (fig. 22). A section $10\ \mu$ above the third level



FIGS. 20-25.—Series of transverse sections of stele of young embryo to show transition; phloem strands numbered 1 to 5, xylem strands lettered a to e.

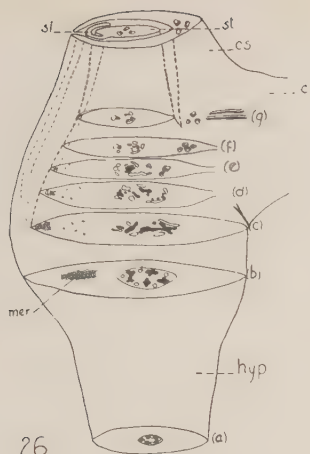
has only four phloem strands, strand 1 having ended at the base of the epicotyl (fig. 23). The xylem strands are located nearer the center than in the section previously discussed; the metaxylem appears as a broken band, owing to lateral extensions right and left, and occupies a tangential position interior to the phloem strands. The fifth section, taken 10 μ above the previous one, shows the xylem located immediately interior to the phloem strands, toward the center of the cotyledon, the portions abutting on phloem strands 2 and 3 being extensions of the halves of the adjacent xylem strands *c* and *d*. The other halves of the xylem strands *c* and *d* are found abutting on phloem strands 4 and 5. The lateral portions of the metaxylem of xylem strand *e* are found right and left, lying against phloem strands 4 and 5 (fig. 24). In a section 30 μ above this one all the bundles are collateral, the xylem, except for a small portion of strand *e*, being located against the phloem and nearer the center of the cotyledon (fig. 25). This portion of *e* at higher levels is found as an isolated strand of xylem.

In another young embryo there are five phloem and five xylem strands in the hypocotyl and only three vascular bundles in the cotyledon. In this instance, near the base of the epicotyl, two of the hypocotyledonary phloem strands and the three xylem strands nearest these are no longer present. The remaining three phloem strands are continuations of the three collateral bundles of the cotyledon. The xylem of these cotyledonary bundles is a continuation of the two xylem strands which alternated with these phloem strands in the hypocotyl.

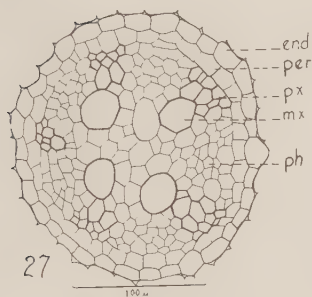
TRANSITION REGION OF SEEDLING

A seedling 47 mm. long was used as a type for study of transition in a young plant possessing a developed stem axis. The zone of transition is short and most of it was found to occur below the point of divergence of the cotyledon from the base of the epicotyl (fig. 26). In a transverse section of the hypocotyl, a little more than 1 mm. below the divergence of the haustorial portion of the cotyledon, the exarch radial arrangement is present (fig. 27).

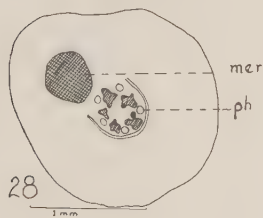
A transverse section through the enlarged portion of the hypocotyl, 230 μ below the divergence of the cotyledon, has a localized meristematic region in the cortex (fig. 28). This is associated with



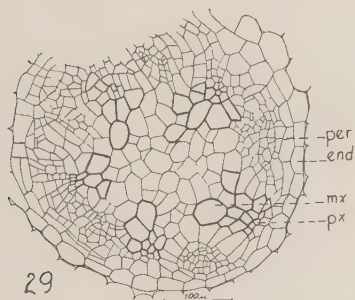
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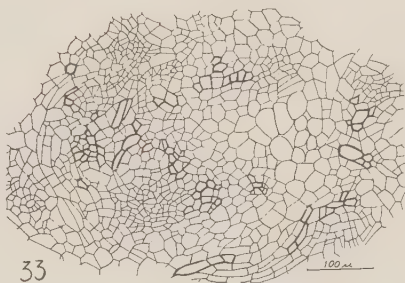
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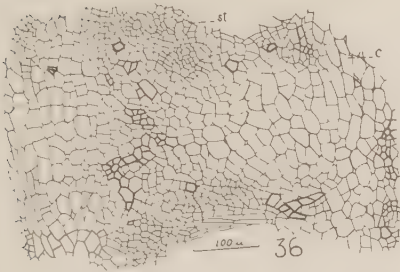
33

FIGS. 26-33.—Fig. 26, diagrammatic reconstruction of part of a seedling to show transition: sections at (a), (b), (c), (d), (e), (f), and (g) represent levels of Figs. 27, 29, 30, 33, 36, 38, and 39. Fig. 27, transverse section of stelar portion of hypocotyl at level indicated by (a) of fig. 26. Fig. 28, diagram of transverse section of hypocotyl at level indicated by (b) on fig. 26. Figs. 29-33, part of a series of transverse sections, at successively higher levels, of transition region (*cs*, cotyledonary sheath; *sl*, scale leaf, *c*, cotyledon; *hyp*, hypocotyl; *st*, stem; *mer*, meristematic region).

the development of the bud which arises in the axil of the first scale leaf of the primary stem. The endodermis and pericycle are no longer evident on the side of the stele adjacent to this area, and the location of parts of the stele varies from the preceding section (fig. 29). The protoxylem points are a little nearer the center of the axis and the innermost metaxylem is situated laterally right and left and lies tangentially interior to the phloem, which maintains its relative positions.

In a section at the level of the divergence of the cotyledon there is a division of the conductive tissue into that part which is to continue into the stem and that part which is to continue into the cotyledon (fig. 30). The cotyledonary portion has four collateral bundles with some isolated xylem strands between these, the whole arranged in a circle. The cauline portion is identified by the location of some phloem and xylem outside of this circle. The arrangement is not clear, but the phloem lies external to the xylem. In the succeeding sections (figs. 31-37), 40, 110, 150, 170, 210, 270, and 310 μ above, there is considerable confusion in the arrangement of xylem and phloem tissues, since portions of many of the bundles appear in longitudinal rather than in transverse sections. This is largely due to the fact that the very short lower portion of the stem develops horizontally as a portion of the rhizome before growing upward as the aerial stem. This is not evident from the external structure because such a small portion of the stem is involved. Extensions of the vascular tissue toward the axillary bud may also account for some of the irregularity. Since the first scale leaf has no vascular tissue, it does not influence this confusion of tissues.

The haustorial portion of the cotyledon contains four vascular bundles. The cotyledonary sheath extending upward contains only three. One of these is larger and represents the upper undiverged portion of two bundles. The bundles of the haustorial portion connect at right angles with the bundles extending vertically from the cotyledonary sheath into the hypocotyl. The isolated xylem strands present in the lower portion of the stem axis (figs. 38, 39) apparently have no significance, since at higher levels they are identified as parts of the xylem of the nearest bundles. This also obtains in the cotyle-



FIGS. 34-39.—Continuation of series of transverse sections at successively higher levels of transition region of a seedling.

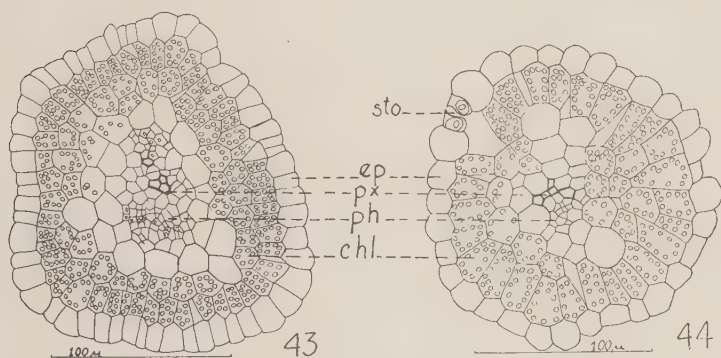
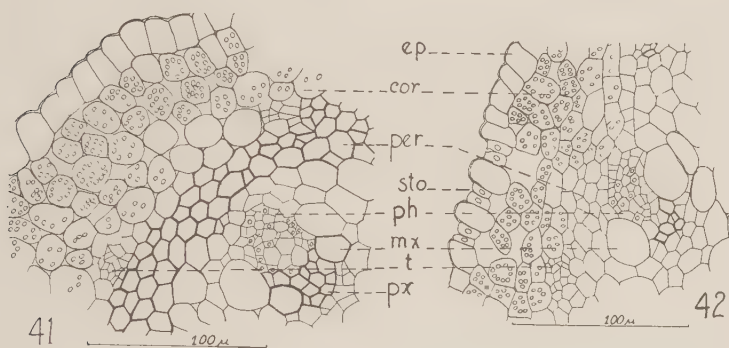
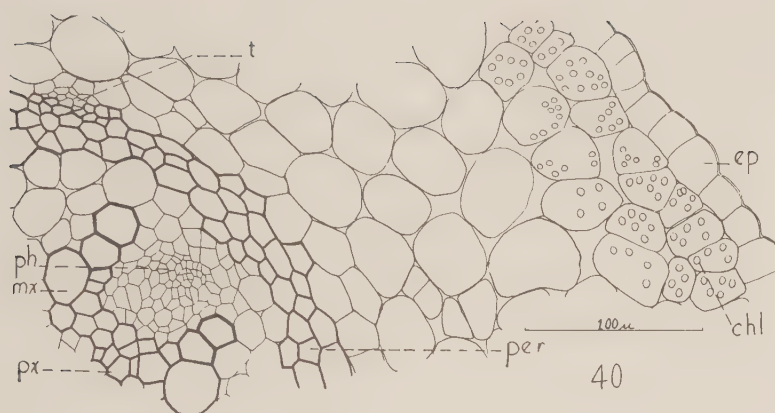
dons where isolated xylem strands are found to be portions of the collateral bundles.

Other seedlings of similar age were examined for transition and were found to be similar to the one described. The transition may be considered a modification of type A of EAMES and MACDANIELS (7) or of type I of VAN TIEGHEM (15).

STEM

The lower portion of the main axis grows out horizontally and forms a small portion of the rhizome before the distal portion extends upward as an aerial shoot. The primary stem is slender and usually less than 2 dm. in height. The lower scale leaves (the first, second, and third) usually contain only branches in their axils. The upper scale leaves may bear both branches and cladophylls (fig. 10).

A transverse section of the primary stem reveals three zones. The first is the cutinized epidermis with stomata. The second is a varying number of rows of large cortical cells, the outer ones photosynthetic and with large intercellular spaces. The third is the stele, which may be divided into three parts: (a) a few rows of pericyclic cells which are strongly lignified in the lower, older portions of the stem and (b) the ground parenchyma located in the center between (c) the irregularly arranged vascular bundles (figs. 40-42). The larger bundles located near the center are the leaf traces, one large bundle associated with each leaf. These bundles are larger and more nearly centrally located in the vicinity of the node where they are diverged from the stele. At lower levels of the stem they are found near the periphery of the central parenchyma, in which region they may end blindly although usually they anastomose with traces of leaves at lower nodes. At the base of the stem there are anastomoses between the bundles of the stem and those of the rhizome. The small bundles which are found peripheral to the pericycle are portions of branch traces. In the upper, younger portions of the primary stem only one new branch trace is found at a node. At lower levels a second trace is differentiated and is present in the main stem at the node. Many anastomoses occur with the common bundles of the stem, but small portions of these branch traces, which do not immediately become part of the central stele, are found in the pericycle



FIGS. 40-44.—Figs. 40-42, parts of transverse sections of lower, middle, and upper portions of primary stem. Figs. 43 and 44, transverse sections of cladophylls (*px*, primary xylem; *mx*, metaxylem; *per*, pericycle; *cor*, cortex; *ep*, epidermis; *sto*, stoma; *t* branch trace; *chl*, photosynthetic area).

through an extent of several internodes before they pass through it and are found in the periphery of the central parenchyma. Here two or three may converge and anastomose with other traces.

The vascular bundles possess a V-shaped xylem arrangement with large reticulated vessels at the apices of the arms of the V and smaller spiral protoxylem vessels directed toward the center of the axis. The arms of the V inclose the phloem.

The bud, arising in the axil of the first scale leaf of the primary shoot, gives rise to a branch the short proximal portion of which forms the continuation of the rhizome, the distal portion the aerial shoot. The bud arising in the axil of the first scale leaf of this second shoot gives rise to the third shoot. As this process is continued, the bases of the aerial shoots form a compact rhizome made up of short internodes. Since the succeeding buds arise alternately right and left, the rhizome has two rows of spears in a close zigzag arrangement. Occasionally accessory buds develop, forming branches of the rhizome.

At the end of the growing season the aerial stems die, leaving scars on the older part of the rhizome. At the tip of the rhizome, however, buds for aerial stems of the next season are already present.

CLADOPHYLLS

The cladophylls are essentially stem structures (fig. 10). They are terete or polygonal in transverse section and have no morphological dorsiventrality. There is a cuticularized epidermis with slightly depressed stomata, the guard cells of which are considerably smaller than the vertically elongated epidermal cells. This differs from ZWEIFELT's description (17) which includes accessory cells associated with the stomatal apparatus. Beneath the epidermis there are two to three rows of palisade cells crowded with chloroplasts. These are followed by the ground parenchyma and from one to four collateral vascular bundles. Two was found as the common number in young cladophylls (fig. 43). A section near the apex of one has a single vascular bundle (fig. 44). In older cladophylls lignified sheaths are developed about the vascular bundles. The vascular connection of the cladophylls with the primary stem is made through an anastomosis of the small bundles of the cladophylls with the large bundle of the scale leaf.

SCALE LEAVES

The sessile scale leaves are approximately triangular in shape, but possess a small, median, ventral prolongation. Usually no vascular tissue or very little is present in the first scale leaf. In the others there are usually four main bundles, two of which extend laterally at the base, and two of unequal size which extend upward in the central region. Small vascular bundles may extend upward from the two lateral bundles. All of these bundles converge into one at the base of the leaf, and vascular connection with the stem is made through this bundle.

Summary

1. The structure of the embryo and the development of the seedling of *Asparagus officinalis* L. are described.
2. The primary root is usually pentarch or hexarch. In its growing point there are two histogens, the inner giving rise to the stele and the outer to the cortex, epidermis, and root cap.
3. Lateral roots are initiated by tangential divisions of cells of the pericycle. Subsequent tangential and radial divisions continue the development.
4. In the development of lateral roots the endodermis becomes active and divides by tangential and radial divisions to form a considerable portion of the "temporary" root cap.
5. Transition from an exarch to an endarch condition of the xylem occurs in the hypocotyl and the bases of the cotyledon and the epicotyl. The transition is complicated by the development of both a part of the rhizome and the first aerial branch from the epicotyl.
6. The rhizome is formed from horizontal outgrowths of the base of the epicotyl and the bases of successive aerial stems.
7. Successive aerial branches arise from buds in the axils of the first scale leaves of the preceding aerial branches.
8. The leaves are scale leaves with one large trace which extends toward the center of the central parenchyma of the stem. From this region the trace gradually diverges outward until, at lower levels of the stem, it is found near the periphery of the central parenchyma. Here it may end blindly but usually anastomoses with traces of leaves of lower nodes.
9. The young branch, arising in the axil of a scale leaf, has small

traces which anastomose with the common bundles of the stem. Small branches of these traces remain in the outer pericycle, through several internodes of the main stem, before they pass through it and come to lie in the peripheral region of the central parenchyma, where they anastomose with other bundles.

10. The cladophylls are essentially stem structures. They arise in clusters in the axils of the scale leaves.

The writer gratefully acknowledges the helpful suggestions and criticisms of members of the Department of Botany of the University of Chicago during the progress of this investigation.

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